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CO-OCCURENCE OF CONGENERIC SPECIES OF MARINE CILIATES AND THE COMPETITIVE EXCLUSION PRINCIPLE: THE EFFECT OF SCALE.

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ABSTRACT. Traditional view based on Darwin and Gause states that closely related species exclude each other more frequently than distant ones. Beginning with Elton, many ecologists regarded the fact, that species -to-genus ratios are lower in insular or local biotas than in corresponding entire pools, as an evidence of this statement. But these arguments are not convincing enough, and there exists an opposite point of view ("coexisting principle").

The present study considers the co-occurence of congeneric species as a statistical phenomenon which could be analyzed in terms of testing the null-hypothesis. According to this hypothesis, congeners co-occur randomly and independently in samples from a total species pool. The hypothesis is verified on free-living ciliates of Russian seas. Data on units of different ecological rank (the whole seas, geographical regions, local communities and separate samples) are compared to the neutral model of "random occurrence". Congeneric species often tend to co-occur more frequently than expected. This general trend, however, appears to be significantly dependent on the focus scale. This is probably the way to resolve the above contradiction. The relative role of factors affecting the species distribution (such as competition, environmental requirements or evolutionary aspects) at different scales is discussed.

Key words: coexistence, species/genera ratio, spatial scale, Ciliata, neutral models.

INTRODUCTION

The problem of co-occurence of congeneric species is closely related to that of species coexistence on the whole. Thus, Charles Darwin stated as early as in 1878: "*As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera.* " Later, Gause (1934) formulated a principle known as the Gause Law or "competitive exclusion principle": "*It is admitted that as a result of competition two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each takes possession of certain peculiar kinds of food and modes of life in which it has an advantage over it's competitor.*" The traditional "competitionistic" point of view based on the authority of Darwin and Gause can be reduced to following sequence of statements:

1. Species closely related taxonomically are also more similar ecologically;

2. Due to this, the competition between congeneric forms should be the most severe;

3. According to the "competitive exclusion principle", closely related species should coexist more rarely than taxonomically distant ones.

To prove the latter statement, species-to-genus ratio, S/G, was often used. This index (more exactly, its inverse value) was proposed as early as in 1901 by plant biogeographer P. Jaccard. He used the S/G ratio as an indicator of diversity of ecological conditions, relating its value to the intensity of interspecific competition (Jaccard 1901, 1922). Jaccard's studies were criticized by Palmgren (1925, 1929) and Maillefer (1929) who showed that increasing species numbers resulted in higher S/G ratios for merely statistical reasons.

Two decades later, the story was repeated: Elton (1946) found that average S/G values for animals and vessel plants were lower on islands than on the continent. He interpreted it as a competitive exclusion of closely related species from the island communities. Williams (1947, 1964), however, concluded that Elton's analysis was erroneous, as he had not take into account the general impoverishment of island biotas.

Having formulated the corresponding null-hypothesis, Williams showed that the observed S/G ratios were not lower on the islands, but even higher than expected. Therefore, according to Williams, the competition hypothesis should apparently be rejected.

Further critical treatment of the subject (Simberloff 1970, den Boer 1980, 1985) led the latter author to formulation of an alternative empirical generalization — the "coexistence principle": "*As taxonomically closely related species usually are also ecologically closely related, related species will be found living together more frequently than could be expected with a random distribution of species*" (den Boer 1985, p. 263).

However, available data are rather controversial, and this gives the ground for estimate of studies in this field as efforts "to find biological interpretations of a statistical artifact" (Jarvinen 1982). In addition, the aspect of scale is often ignored: the results obtained from local samples are transferred to the biogeographical level and vice versa. There is another disputable point, i.e., the construction of correct null-hypotheses and statistical testing of data for non-randomness.

The present study is another effort to resolve contradictions. Free-living ciliates were chosen as a model subject (notably, those were experiments on ciliates that led Gause to reveal his principle). A co-occurence of taxonomically closely related species was treated as an integral phenomenon to be statistically described to reveal its general tendencies. The focus was on the factor of scale. Thus the question was: could we, basing on the numbers of genera and species, consider the available local species lists as random samples from the given source fauna?

Formulating this more strictly, our "neutral model" was based on the following null-hypotheses:

1. S/G ratios for real species lists of various size coincide with those for random samples from the total pool; and

2. S/G ratio value depends only on the sample volume, and other factors do not affect this dependence.

These hypotheses are tested in the present study in sequence and independently.

MATERIAL AND METHODS

INITIAL DATA. Species numbers are usually tallied from check-lists of species from particular regions. This is complicated by some essential problems (see Connor and Simberloff 1978):

a. All species are usually treated as biologically equivalent, whether rare or common, or mono- or polymorphic ones. The latter aspect may be of particular importance for Ciliata, among which the species complexes exist, that apparently are indistinguishable morphologically, though exhibit distinct patterns in their microdistribution (Borror 1980).

b. The criteria indicating the presence or absence of a species from a particular locality are "ambiguous" (Connor and Simberloff 1978). This also may be significant for such highly mobile species as protozoans. Some forms are ecologically "rapidly transient", and this leads to very high rates of species turnover in communities (Schoener 1983, Azovsky 1988).

c. Different localities may receive unequal collecting efforts, and may be studied at different times. If so, the comparison of species numbers from several localities yields biassed results, particularly for such patchy distributed organisms.

d. Finally, the results of species registration and identification by different scholars may considerably vary. The systematics of Protozoa is rather complex and has not been yet completely established. Recent revisions of both particular taxa and the whole group make it difficult to compare data from different sources.

These problems handicap the obtaining reliable data for our purpose. To minimize the above biases, such data should meet at least the following requirements:

a. They should represent species lists obtained for units of various type and scale, that are located within a particular faunistic complex;

b. Total fauna of ciliates should be studied more or less completely and systematically;

c. All data should be obtained by the same researcher (or a group of researchers), using the same methods.

The present study is based on the following data, which meet the above criteria fairly adequately.

I. Data obtained by I.V. Burkovsky and his collaborators, including the author, on the fauna of free-living ciliates of the White Sea (the results of faunistic and ecological investigations of over 25 years, presented in more than 30 papers, including a monograph (Burkovsky 1984); and some unpublished data). The material includes data on ciliates of the Kandalaksha Gulf, ranging from biotas of different biotopes and bay areas to separate samples. Data on species common for the White Sea and some other seas are also included.

II. F.G. Agamaliev's data on the Caspian Sea fauna (results of over 25 years systematic investigations, presented in more than 35 papers including a monograph (Agamaliev 1983)). The

material includes data on ciliates of various biotopes, geographical areas of the sea, particular bays and islands. Data on species common for the Caspian fauna and that of some other seas are also included.

III. Data on ciliates of Dalnezelenetskaya Inlet (the Barents Sea) obtained at the Biological Station of Murmansk Marine Biological Institute (fauna of two sections of sand littoral — the Dalnij Beach and the Oscar Bay).

The list of data sources is given in Appendix. In some cases, the species lists were revised, taking into account the changes in systematics of particular taxa, introduced by the authors themselves later (renaming or changing the status of species). Major correction concerns such groups as Trachelocercidae (the White and the Barents Seas), *Euplotes* and *Diophrys* (the Caspian Sea), and Tintinnida (the White Sea). Data from other sources were rejected due to reasons stated above.

The following variables were determined for each data set: SN — total number of species; GN — total number of genera; REGION — conditional variable, equal to 0 if the data are related to the limited region (e.g., a section of littoral, particular island, or small bay), or 1 if sampling area is combined; ISLAND — conditional variable, equal to 0 for island fauna and 1 if the data are related to plankton or were not collected on an island; BIOTOP — conditional variable, equal to 0 if the data are related to a single biotope type, and 1 if they are related to various types.

The biotopes were distinguished by the type of substrate (very fine sand, fine, medium, coarse sand, gravel, algal mud and algae aggregates, macrophytes, stones and rocks, coastal "bathes", water mass), and also by vertical: supralittoral zone, littoral, depths of 0-10 m, 10-50 m, over 50 m. See primary sources in Appendix for details.

MODEL DESCRIPTION AND STATISTICAL PROCEDURES. A theoretically expected number of genera in random samples from the known total pool can be calculated basing on the hypergeometric distribution (Polya 1930). However, these calculations are rather cumbersome and do not give adequate estimates of possible dispersion. Hence, to estimate the parameters of a neutral model, we used an analog of the rarefaction method (Heck et al. 1975, Simberloff 1978). The procedure was as follows. For each initial source pool of species, regarded as a parent population with a general number of species S_{total}, the S/G_{total} ratio was calculated. Then random samples of the given volume were taken from this pool (each by 50 retries) and the average value of S/G_{model} and its standard deviation were determined. The dependence of S/G_{model} on the species number SN in the sample was studied by regression analysis of averaged data (Draper and Smith 1981). A similar dependence was also studied for actual data (S/G_{real}) by the multiple regression method. The conditional variables BIOTOP, REGION and ISLAND were also included in the model, as well as terms reflecting the interactions between variables (Draper and Smith 1981). A modified Student's t-criterion was used to compare regression coefficients (Urbakh 1975). All calculations were made, using the statistical package SYSTAT (Wilkinson 1987).

RESULTS

TEST OF RAREFACTION MODEL. To test the model, 4 different total species pools on various biogeographic scales were used:

1. The world-wide fauna of marine free-living ciliates (136 genera, 923 species) (Burkovsky 1970, Agamaliev 1983);

2. The Caspian Sea fauna (132 genera, 439 species);

3. The benthic fauna of the Kandalaksha Gulf of the White Sea (70 genera, 210 species);

4. Psammophilous ciliates of the Dalnezelenetskaya Inlet of the Barents Sea (45 genera, 123 species).

For all above sets, the average values of

Table 1. Coefficients of linear regression of S/G ratio on species number in the sample ("neutal model").

Total species pool	a model (±SE)	b model (±SE)	R
World Ocean S total = 923 S/G total = 6.667	1.625 (±0.05)	0.00581 (±0.00016)	0.995
Caspian Sea S total = 439 S/G total = 3.326	1.063 (±0.008)	0.00530 (±0.00005)	0.999
White Sea S total = 210 S/G total = 3.000	1.039 (±0.0063)	0.00952 (±0.00007)	0.999
Barents Sea S total = 123 S/G total = 2.733	1.0051 (±0.011)	0.01428 (±0.00021)	0.999

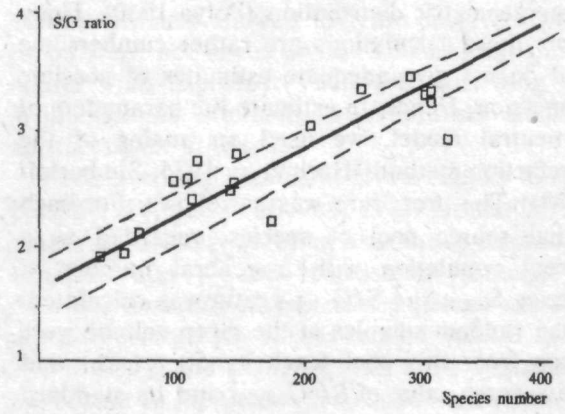

Fig. 1. Average number of species per genus in faunas of free-living ciliates of oceans and seas of the world.
Dots — real data, solid line — the model (random samples from the World Ocean fauna). Dashed lines show the standard error limits for model data.

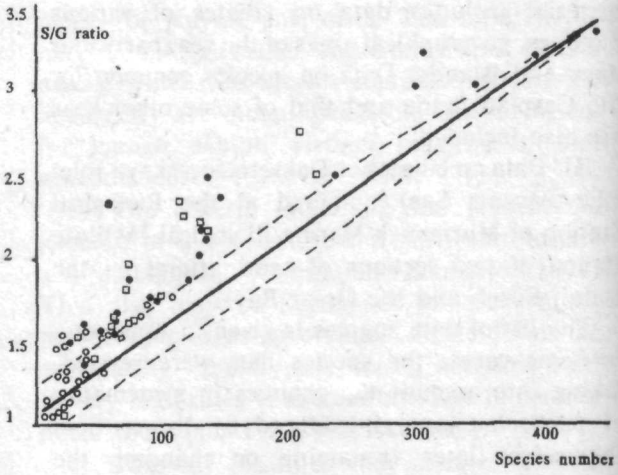

Fig. 2. Average number of species per genus in samples from the Caspian Sea fauna.
Squares — species from other seas, common with the Caspian fauna; dashed circles — regional biotas; empty circles — local biotas. Solid line — the model (random sampling). Dashed lines show the standard error limits for model data.

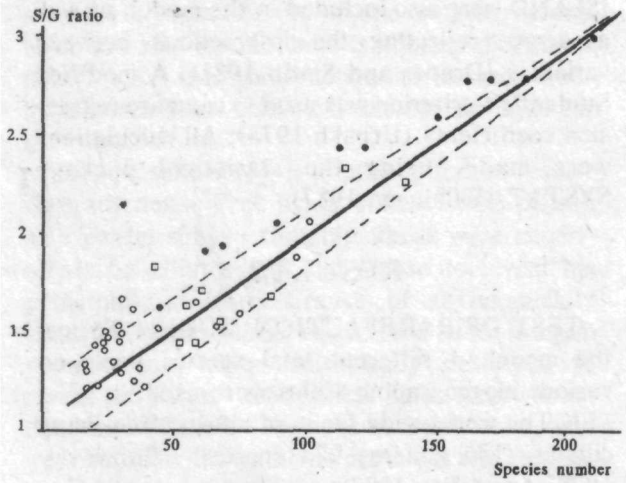

Fig. 3. Average number of species per genus in samples from the White Sea fauna.
Symbols as in Fig. 2.

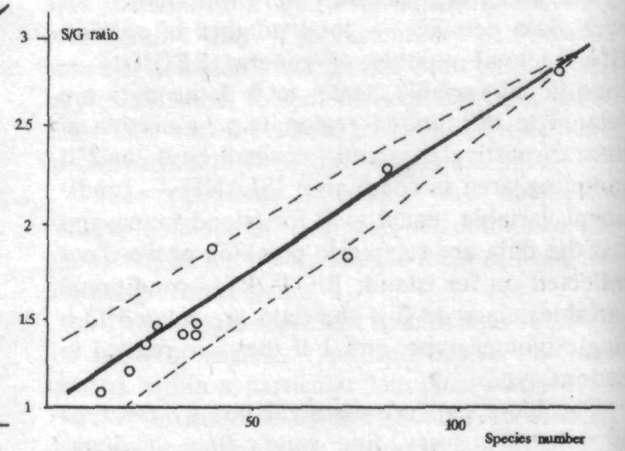

Fig. 4. Average number of species per genus in samples from the fauna of the Dalnezelenetskaja Bay of the Barents Sea.
Symbols as in previous figures.

S/G_{model} appeared to be almost linearly related to the species number in sample SN. The percentage of dispersion explained by linear regression in the form: $S/G_{model} = a + b * SN$ exceeds 99 %. The results of the calculation are given in Table 1 and show good acceptability of linear approximation of rarefaction model. Therefore, we subsequently used linear "neutral models" with the coefficients from Table 1 to test null-hypotheses.

COMPARISON OF THE ACTUAL AND MODEL VALUES OF S/G RATIO. To test the first null-hypothesis (see Introduction), it is necessary to know whether the mean number of species per genus in the given species list differs significantly, and in what direction, from the expected for a random subset of total pool. In other words, pair comparison of S/G_{real} and S/G_{model} values for each set of species is a generally accepted test. The results of such a comparison for our data are given in Table 2.

As it is seen from the Table 2, the major part of actual values exceeds the model ones, but only less than one third of them differs significantly. In other words, most species subsets have more congeners than it would be expected, though few have significantly more. The higher co-occurence of congeners is greatest in the Caspian ciliates inhabiting several seas, and lowest — in ciliates of the Barents Sea inlet sand littoral. It is generally accepted that small deviations from expected values (less than 2 standard deviations) can be neglected (Simberloff 1970, Jarvinen 1982). Thus, pair comparisons reveal only a

Table 2. The pair comparison of observed and expected values of S/G ratio for various species lists.

Total species pool	Total number of subsets (species lists)	The percent of cases, in which:			
		S/G real less than S/G model	Significantly less on 95% level	S/G real greater than S/G model	Significantly greater on 95% level
World Ocean	18	33.3	11.1	66.7	16.7
Caspian Sea (species of other seas, common with the Caspian Sea)	15	—	—	100.0	80.0
Caspian Sea (inner subsets)	56	17.9	—	82.1	37.5
White Sea	37	24.3	—	75.7	24.3
Barents Sea	10	70.0	10.0	30.0	—

slight trend for congeners to be correlatively distributed, but a small number of significant deviations prevents this result from being clearly interpretable.

DEPENDENCE OF S/G RATIO ON THE SPECIES NUMBER — COMPARISON WITH A MODEL. Deviations of S/G ratio from the expected values may be statistically insignificant but constant. Here some factor of non-random nature is apparently present. We tried to separate the possible effect of these factors from the influence of sample size, comparing the corresponding regressions (Figs. 1-4; Table 3). It is evident, that the slopes of regression curves for the model and actual samples practically coincide (except the White Sea), i.e. values of S/G ratio grow with increasing species number in accordance with our neutral model. However, free terms differ. Only for situations extreme in terms of scale — the fauna of seas (Fig. 1, the World Ocean as a total pool) and the Barents Sea littoral (Fig. 4, one of the bays of the Eastern Murman as a total pool) — the "actual" and "model" lines practically coincide. In all other cases, observed values are consistently higher than the model curves. Only at low species numbers, reverse deviations are clearly manifested. These differences are statistically highly significant.

Thus, the first null-hypothesis formulated in the Introduction:

"*S/G ratios for real species lists of various sizes coincide with those for random samples from the total pool*"

can be rejected for three total pools out of five. For closely related ciliate species, the tendency to occur in the same species lists is a statistically significant phenomenon, *and the degree of its manifestation does not depend on the number of species in the list.*

S/G RATIO, SAMPLING SCALE AND SAMPLES NATURE. The species lists under study are rather heterogeneous. They vary from separate samples up to the sea faunas. Does the sampling scale affect its taxonomic diversity? To clear up this question, a more detailed regression analysis was done, including sample characteristics as independent variables (Table 3). Nonlinear terms reflecting possible interactions between variables appeared to be insignificant and can be rejected. The "island effect" (for the Caspian ciliates) also proved to be negligible: island samples themselves do not differ significantly from planktonic or coastal ones. The biotopic diversity also does not significantly affect the S/G ratio, i.e. the percentage of congeners does not depend on whether the given set of species is found in a single or in various types of biotopes.

At the same time the "regional effect" contribution appeared to be significant: when species pool integrates the biotas of several local habitats, the percentage of congeneric species is apparently higher than that in a single locality with the same number of species. It should be noted in particular that *degree of the effect manifestation is not a function of sample size*: as the species number increases, "local" and "regional" values of S/G ratios grow at the same rate (according to the "neutral" model), but the former ones are always lower than the latter. Thus, the second null-hypothesis :

"*The S/G ratio value depends on the sample value only, and other factors do not affect this dependence*"

is also to be rejected. Instead, alternative statements can be formulated:

a. The S/G ratios for actual sets of ciliate species systematically deviate from those for random samples from total pools ;

b. The degree of deviation depends on the ecological scale of the units under study rather than on the species number.

In units of intermediate range ("regional"

Table 3. Multiple linear regression for real S/G ratio data.

Total species pool	Independent variables					R	Difference from the model		
	Intrsept a	SN b	REGION c	BIOTOP d	ISLAND e		a	a+c	b
World Ocean	1.754 ±0.152 p<0.001	0.005 ±0.001 p<0.005	—	-0.587 ±0.393 p<0.39	—	0.977	ns	—	ns
Caspian Sea-I	1.272 ±0.095 p<0.001	0.006 ±0.0009 p<0.001	—	0.060 ±0.096 p<0.54	—	0.916	**	—	ns
Caspian Sea-II	1.046 ±0.056 p<0.001	0.008 ±0.0015 p<0.001	0.259 ±0.105 p<0.02	0.041 ±0.172 p<0.85	0.065 ±0.069 p<0.35	0.966	*	***	ns
White Sea	1.240 ±0.038 p<0.001	0.007 ±0.0011 p<0.005	0.485 ±0.168 p<0.007	0.061 ±0.261 p<0.82	—	0.967	***	***	*
Barents Sea	0.963 ±0.071 p<0.001	0.014 ±0.0013 p<0.001	—	—	—	0.966	ns	—	ns

The form of equation is:
S/G = a + b*SN + c*REGION + d*BIOTOP + e*ISLAND + ...
The terms of higher orders are not addused (all non-significant).
Significance level of real/model terms difference: * — p<0.05
** — p<0.01
*** — p<0.001
ns — not significant

samples from sea fauna, biotopes types), related species co-occur more frequently than species of different genera. It is not observed neither for units of low rank (local communities and given samples), nor for higher rank units (the biotas of particular seas as samples from the World Ocean fauna).

DISCUSSION

Let us now turn to the biological interpretation of our statistical findings. What factors can modify the S/G ratio in the above stated way? We mentioned two major of them in the Introduction:

1. The similarity of ecological requirements of congeneric species (which increases S/G ratio); and
2. Interspecific competition (acting in the opposite direction).

A large-scale distribution of species, their presence or absence in a particular geographical region is mostly determined by environmental requirements, i.e. availability of suitable biotopes. Since congeneric species are similar in this respect, they are to be distributed by connected complexes. Under certain conditions, species of certain genera are found more frequently: this is a fact apparent to each biologist.

As to competition and species replacement connected with it, it is unlikely that the whole unit of such a scale could be an arena for these processes. The population of large territories is composed of many local populations, interactions between those are apparently rather limited. Anyhow, the complete exclusion of one species of ciliates by another from the whole sea or from a part of it is too long process to be revealed in our data. As a result, the co-occurence of congeneric species on the regional scale is significantly increased.

Conversely, in local habitats, the species composition is usually determined not by environmental requirements (the species have passed through this "filter" at the regional level), but mostly by biological interactions within the community as well as by chance. Earlier (Azovsky 1989 a, b) the leading role of interspecific competition and niche separation was demonstrated in the forming structure of local communities of ciliates. Therefore the significant lowering of the proportion of congeners in local communities and in samples from them is explained by us just by intensive competition between closely related species.

Why the effect of competitive exclusion "in its evident form", i.e. **decreased** co-occurence of congeners, is, however, observed so rarely, although since Elton it has been looked for so persistently? In our case too, the S/G ratio rarely fell significantly lower than the level of "neutral model". According to den Boer, this could be interpreted in two ways: "*...either because competition does not influence distribution significantly, or because competition does equally affect the distribution patterns of both closely related and unrelated species.*" (den Boer 1980, p. 284). Den Boer himself consistently adhered

Fig. 5. Scale effect in congeneric species distribution (an example).
20 assumed species of 4 genera (A, B, C and D) are distributed in 9 microhabitats ("local" level), united in 3 areas ("regional" level).

Habitat:	AREA I			AREA II			AREA III		
	1	2	3	4	5	6	7	8	9
Gen. A	A1	A2, A3	A4, A5	A4		A5			
Gen. B	B1, B2	B2	B3	B3	B4	B5			
Gen. C				C1	C2, C3	C4	C3	C4	C5
Gen. D							D1, D2	D2, D3	D4, D5

		In Habitats:	In Areas
Mean S/G ratio:	Expected	1.26±0.35	2.37±0.21
	Observed	1.39±0.30	3.67±0.47

the former interpretation. He rejected the latter explanation since he believed that "*taxonomically closely related species are also ecologically closely related*" (Ibid. p. 285). However, presumably it is not always the matter. A special study on psammophilous ciliates (Azovsky 1990) showed that species of the same genus on the average have more similar ecological niches than randomly chosen species have. But the differences are small and statistically nonsignificant.

Illustrative examples of subtle but essential differences are found in some ciliates of the order Karyorelictida. They are typical inhabitants of interstitial space, with a fairly narrow and specific environmental orientation. However, in local communities, congeneric species show clear differences in food and/or microhabitat selection (Fenchel 1968, Finlay and Berninger 1984, and our own data).

Besides, the competition in ciliates communities has a diffuse nature, i.e. the integral pressure of the entire community on a particular population is important. The contribution of congeneric species to this integral pressure is usually too small to lead to significant shift in niche or, moreover, to complete exclusion of one of them. *Therefore the local competition, superimposing the regional conjugation, cannot completely overcome its "background" effect.* An invented example illustrates this situation — the distribution of 20 species from 4 genera among 9 "habitats" in 3 "regions" (Fig. 5). The observed S/G ratios at the "regional" level are significantly higher than the expected ones. At the level of particular habitats, these values are practically equal. But S/G ratios do not fall lower than the neutral model level, since the regional coexistence camouflages local segregation of congeners.

The effect of the two considered variables (ISLAND and BIOTOP) appeared to be nonsignificant. The lack of "island effect" is generally clear: for ciliates, there is no essential difference between an island and any other part of the sea bottom in their degrees of isolation. The reasons for the second variable nonsignificance are not so apparent. Presumably this also accounted for by the manner of the environment partition by ciliates. The small size, high adaptability and short generation times made it possible for many of these creatures to inhabit a wide environmental spectrum, although they divide each available biotopes between them in a fairly delicate manner (Burkovsky 1987, Fenchel 1987, Azovsky 1989 a, b). It was demonstrated (Azovsky 1989 c) that the range of biotopes occupied by given species is inversely correlated with the width of its realized niche in each biotope. Due to that, intra- and intergeneric partition of the environment is accomplished by ciliates on finer ecological scales than that of our rough classification of biotopes. The effect of such partition should be reflected by the REGION rather than BIOTOP variable.

Another point that requires comment is the absence of reliable differences from the neutral model on the level of sea faunas. One would think that such differences, so pronounced within the sea, should be more pronounced on further increasing scale. However it is not the matter. In faunas of particular seas, congeneric species of one genus occur no more frequently than in random samples from the Ocean fauna, in spite of their conjugation in particular regions of the White and Caspian Seas and even in pairs of seas (ciliates, common with the Caspian Sea). In our opinion, this can be explained by the effect of evolutionary factors. The faunas of

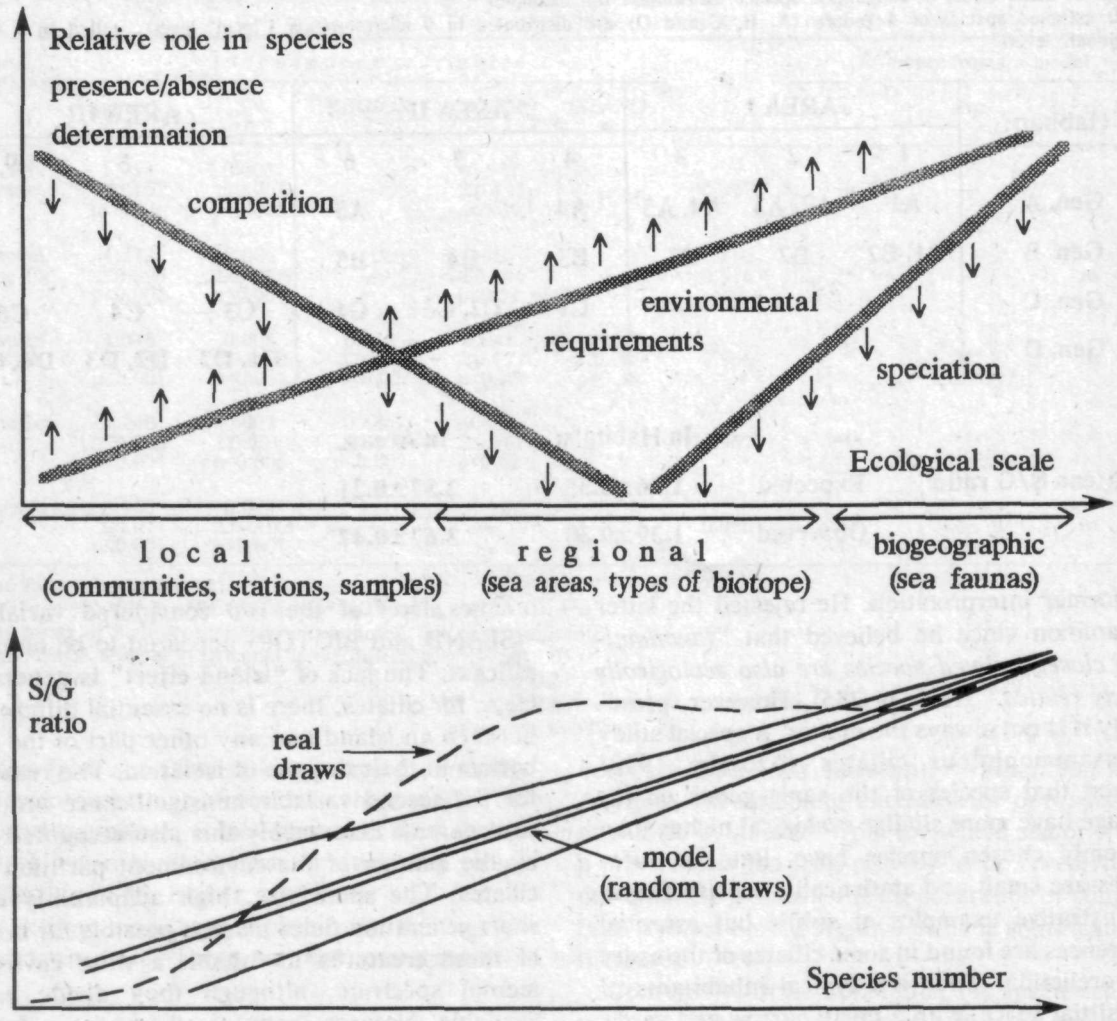

Fig. 6. Change of comparative role of ecological factors in dependence on the scale of species set (schematically). Vertical pointers (at the upper part) show the direction in which the factor affects S/G ratio (at the lower part).

particular seas, as biogeographic units, are derived not only from reciprocal colonization, but also from speciation processes, operating independently. The total species pool is replenished by unique elements, i.e., by new species. This factor affects our estimates in the direction similar to that of competition (but, of course, on completely different scales of space and time). It increases S/G_{total} and thus reduces the gap between the observed and expected values in particular seas, "lowering" the actual points on the model line. *Thus, for units of such biogeographic scale, the fitting of data to the random model may appear to be not the effect of "random" sampling, but the result of mutual compensation of opposite factors, both ecological and evolutional.*

The observed deviations from model values in S/G ratios of particular faunas can also be explained by the fact that they have been investigated to a different extent. Really, the proportion of congeners is smallest (as compared to the expected one, see Fig. 1) in the best-studied Baltic and Mediterranean Seas. At the same time, a significantly higher percentage of congeners occurs in faunas of the Japan Sea, the North and the Barents Seas, which were markedly less studied at the time when the checklists were compiled. At superficial study, widely distributed and well known abundant forms of polyspecies genera usually predominate in the faunistic lists, and only detailed investigations enlarge the list by rare and endemic forms usually with few number of species in the genus. Indeed, in the first two mentioned above seas, over one forth of all species are endemics, and less than a half are widely distributed. Conversely, in three poorly studied seas, the bulk of known species (about 75 %) is represented by widely distributed forms, while endemics comprise less than 10 % (the data from Burkovsky 1970, Agarova et al. 1976).

Thus, as the World fauna becomes more studied, the S/G ratio is expected to decrease for particular seas and to increase for the fauna as a whole.

Thus, the average number of species per genus, as an indicator of taxonomic diversity, depends on the scale of the species set under investigation. Here it becomes clear why in previous studies the competition was mainly revealed at the level of local communities, while the coexistence of congeners — chiefly at the regional level (S /G ratio exceeded the expected values) (Williams, 1947, 1964, Simberloff 1970; Connor and Simberloff 1978, den Boer 1980, 1985, 1986, Jarvinen 1982). After analysing a large number of investigations, carried out on various scales, Connor and Bowers (1987) came to a similar conclusion: "...It appears that demonstrating that interspecific competition has spatial consequences is *more difficult at regional and biogeographic scales than it is at habitat scale*" (p. 221).

However, it does not imply that the "competitive exclusion principle" and "coexistence principle" must exclude each other. They can perfectly coexist since we can point out an area for each of them, where the processes postulated by them will dominate (Fig. 6). Thus, the contradiction between the viewpoints of Gause — Elton, on the one hand, and those of Simberloff — den Boer, on the other, can be eliminated taking into account the scale of examining the phenomena.

In conclusion, I would like to cite a statement by E.C.Pielou, which appears quite appropriate: "*Of course, qualitative measures of statistical properties rarely (if ever) provide sensationally new knowledge by themselves. At the same time, they may introduce an objectivity into results, which otherwise would be mere intuitive theorizing concerning the real meaning of some data, which are hardly interpreted.*" (Pielou, 1988, p. 59; cited in reverse translation from Russian).

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APPENDIX

LISTS OF FAUNISTICAL DATA SOURCES

I. CASPIAN SEA

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II. WHITE SEA

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III. BARENTS SEA

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Совместная встречаемость родственных видов морских инфузорий и принцип конкурентного исключения: влияние масштаба

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Таксономически близкие виды чаще должны вытеснять друг друга — это классическая точка зрения, покоящаяся на авторитете Дарвина и Гаузе. В качестве одного из доказательств многие экологи, начиная с Элтона, указывали, что отношение числа видов к числу родов в островных или локальных биотах ниже, чем в соответствующих полных видовых пулах. Однако их аргументы оказались недостаточно убедительны, и противоположная точка зрения ("принцип сосуществования") также существует.

В настоящей работе совместная встречаемость родственных видов рассматривается как статистический феномен, который можно анализировать в рамках проверки нуль-гипотез. В соответствии с такой гипотезой, встречаемость видов одного рода в выборках из общего исходного пула видов является статистической величиной и зависит лишь от размеров выборки. Гипотеза проверяется на примере свободноживущих инфузорий морей СССР. Данные по экологическим единицам различного ранга (моря в целом, их географические районы, локальные сообщества и отдельные пробы) сопоставляются с нейтральной моделью "случайной встречаемости". Родственные виды встречаются совместно в общем чаще, чем ожидалось. Обнаружена зависимость общей тенденции от масштабов рассмотрения, что может разрешить вышеупомянутое противоречие. Обсуждается относительная роль влияющих на распределение видов факторов (таких, как конкуренция, требования к среде обитания или эволюционные аспекты), в разных экологических масштабах.